Co-existence and niche segregation of three small bovid species in southern Mozambique

Prins, HHT; de Boer, WF; van Oeveren, H; Correia, A; Mafuca, J; Olff, H; Boer, Willem F. de

Published in:
African Journal of Ecology

DOI:
10.1111/j.1365-2028.2006.00619.x

Publication date:
2006

Co-existence and niche segregation of three small bovid species in southern Mozambique

Herbert H.T. Prins[1]*, Willem F. de Boer[1,2], Herman van Oeveren[1], Augusto Correia[2], Jorge Mafuca[2] and Han Olff[1,3]

[1]*Resource Ecology Group, Wageningen University, Bornsesteeg 69, 6708 HM, Wageningen, The Netherlands,* [2]*Department of Biological Sciences, Eduardo Mondlane University, C.P. 257, Maputo, Mozambique and* [3]*Laboratory for Plant Ecology, University of Groningen, P.O. Box 14, 9750 AA, Haren, The Netherlands*

Abstract

Niche segregation among three small antelopes – red duiker, common duiker and suni – was investigated in a coastal savanna woodland/forest mosaic. It was expected that these similar-sized concentrate selectors would show differentiation in diet choice to decrease competition. Diet composition did not vary significantly among the different vegetation types. For all three antelope species, the number of dietary items was large, with a minimum of 70 different food items per species. Dietary specialization was low, with only 10% of the food items being exclusively used by each of the species. The ranks of food items were positively correlated among species in the wet season, but not in the dry season. Diet breadth significantly decreased in the dry season. The use of exclusive species was significantly larger in the dry season with lowest values recorded for the common duiker. Diet overlap in the wet season was considerable, but significantly decreased in the dry season, the time of food scarcity. The dry season data showed evidence for niche segregation, although this was not based on displacement. As niche segregation in the dry season was coupled to a random apportionment of diet items among antelope species, it cannot be interpreted as the result of competitive displacement.

Key words: antelope, competition, diet overlap, faecal analysis, resource partitioning

Résumé

La ségrégation des niches chez trois petites antilopes - le céphalophe du natal, le céphalophe de Grimm et le suni – fut étudiée dans une forêt de la savane littorale/mosaïque forestière. On s'attendait à voir une différentiation dans les choix alimentaires afin de réduire la compétition parmi ces sélecteurs de concentrés de taille semblable. La composition alimentaire ne changeait pratiquement pas parmi les différentes classes de végétation. Chez les trois espèces d'antilopes le nombre d'éléments alimentaires fut grand, avec un minimum de 70 aliments différents par espèce. Le niveau de spécialisation alimentaire fut bas, avec seulement 10% des éléments alimentaires consommés en exclusivité par chaque espèce. Le grade d'éléments alimentaires fut corrélé de manière positive parmi les espèces pendant la saison des pluies, et moins pendant la période sèche. L'étendue de leur diète diminua d'une manière importante pendant la période sèche. L'utilisation d'espèces exclusives fut beaucoup plus importante pendant la période sèche, avec les plus basses valeurs chez le céphalophe de Grimm. Le chevauchement d'aliments pendant la saison des pluies fut majeur, mais diminua d'une manière importante pendant la période sèche, quand les aliments furent difficile à obtenir. Les données obtenues pendant la période sèche démontrèrent des preuves d'une ségrégation des niches, quoique ceci ne fut pas basé sur le déplacement. Puisque la ségrégation des niches pendant la période sèche fut liée à un partage aléatoire d'éléments alimentaire parmi les espèces d'antilope, ceci ne peut pas être interprété comme le résultat du déplacement compétitive.

Introduction

Related species that live together are thought to show specialization or niche differentiation to avoid competition. Niche differentiation may result from habitat segregation, morphological adaptations (e.g. of the gut to feeding browse or grass), or behavioural adaptation (e.g. specialized dietary adaptations). Morphological specialization

*Correspondence: Tel.: +31 317 483900; Fax: +31 317 484845; E-mail: herbert.prins@wur.nl

could be advantageous if it diminishes resource competition with other species. However, it may result from historical interspecific competition, or the 'ghost of competition past' (Connell, 1980). This makes finding causes of niche segregation difficult, because competitive forces in the past are difficult to appraise.

Studies of interaction between herbivores in multi-species assemblages are scarce, yet there has been considerable speculation about the actual mechanisms of niche partitioning (Jarman & Sinclair, 1979; Jenkins & Wright, 1988; de Boer & Prins, 1990; Mathur, 1991). Hence, it is difficult to prove whether an ecological segregation implies a lack of interaction, or an explicit response to competition. Most proof for competition among sympatric herbivores is based on circumstantial evidence (Keiper, 1985; Putman, 1996). Numerical analyses of population responses are desirable to confirm the existence of competition (Prins, 1996). Experimental studies are scarce, and most evidence for competition between herbivores comes from systems in which livestock was introduced, displacing native herbivores (Loft *et al.*, 1987; Loft, Menke & Kie, 1991; Ragotzkie & Bailey, 1991; Voeten & Prins, 1999; Prins, 2000; Mishra *et al.*, 2004).

Theoretically, competitive interactions among herbivores are predicted to be the most severe between species that have the same feeding style and similar body weights; when body weights are different, it is predicted that species may partition resources by size and quality, such that each species has exclusive resources (Belovsky, 1986; Prins & Ol, 1998; Ritchie & Ol, 1999). In this study, we quantified niche segregation among three small antelopes (red duiker *Cephalophus natalensis* Smith, common duiker *Cephalophus grimmia* L., and suni *Neotragus moschatus* von Dueben), all bovids (Kingdon, 1982). These antelopes co-exist in the same habitat despite their similar size. Consequently, we explored their diet and habitat use in three habitats in southern Mozambique to determine how they partition resources.

Material and methods

Study site

The Maputo Elephant Reserve in southern Mozambique, comprises 800 km^2. The average annual rainfall is 690–1000 mm (DNFFB, 1997). Two different seasons are discerned – a hot rainy season (October to March), and a cooler dry season (April to September). The vegetation is classified into several broadly defined vegetation communities (de Boer *et al.*, 2000; Matthews *et al.*, 2001) of which three are important for small antelopes. The grass plains are low-lying plains that are seasonally inundated, characterized by the absence of trees. Sand forest is found in the southern and eastern undulating part of the reserve and has developed around lakes and on top of the sand dunes; typical understorey species are *Panicum deustum*, *Phyllanthus* sp. and *Acacia kraussiana*. Savanna is found on the slopes between the dune sand forests patches; it has a well-developed herbaceous layer interspersed with trees.

The small bovid assemblage

The most abundant antelopes are reedbuck (*Redunca arundinum* Boddaert) and duiker species (Tello, 1973). Common duikers are abundant in the reserve, preferring savanna and sand forest. The reserve is further used by a small elephant (*Loxodonta africana* Blumenbach) population (de Boer *et al.*, 2000). Large predators, or other larger grazers and browsers have gone extinct from the area.

These three small, 'primitive' antelope species are not dependent on water, all territorial, and forage on a wide range of browse items, often on fallen leaves, fruits and pods (Kingdon, 1982, 1997; Lawson, 1989). The similarity in diet overlap was also noted by Hofmann (1973) regarding suni and red duiker in Kenya. The three species have rather similar weights, and all three are concentrate selectors with high fermentation rates (Kingdon, 1982). The questions are, thus: (i) how these three species are able to co-exist, (ii) to what extent these species have segregated their diets, and (iii) whether this segregation is a strategy to prevent niche overlap and reduce competition.

Suni (4–6 kg: Kingdon, 1997; 8 kg: Hofmann, 1973) mainly live in coastal shrub and sand forest; they do not need to drink water but can survive on the moisture content of their food (Somers, Rasa & Apps, 1990; Kingdon, 1997). The two Cephalophini duiker species(Kingdon, 1997), the red duiker and the common duiker, are territorial antelopes of group A of Jarman (1974). The red duiker (12–14 kg, Kingdon, 1997) is an opportunistic feeder on fruits, flowers and foliage. It does not need to drink water (Estes, 1991). Kingdon (1982) considered the red duiker to be most similar to the common ancestor of all duikers, and classified it as a generalized duiker species. According to Kingdon (1982), its feeding is opportunistic. The common duiker is slightly larger, 12–25 kg, and does not need to drink water either (Kingdon, 1997). Hofmann (1973) gave a lower weight range, namely 12–16 kg. Its food is very varied (Kingdon, 1982, 1997).

Methods

The diet of the antelopes was studied using faecal analysis (Stewart & Stewart, 1970; Field, 1972; Soane, 1980; Bhadresa, 1986). Plant samples for the reference collection were taken in March 1994 of all common plants in the Reserve as well as those listed by Tello (1973) as potential forage plants, and plant with signs of grazing encountered during field work. Samples were stored in 10% nitric acid and processed in the laboratory following Field (1972), Soane (1980) and Bhadresa (1986), mounted on glass slides, and stained with gentian violet. Several slides were prepared of both abaxial and adaxial epidermis layers of each plant species and photographed through a microscope. Epidermis cells are different between species, and between fruit, leafs, or bulbs (Stace, 1965), so identification was done per plant part (or diet item) and not per species, as diet overlap could be avoided by choosing different plant parts.

Faecal samples (a sample being a pile of fresh pellets, <12 h old, of which about 10 different pellets were collected and mixed) were collected in three different periods: March 1994 (late wet season), November 1994 (early wet season) and September to October 1995 (dry season). Identification and age of faecal samples was analysed by experienced rangers, using the method of Walker (1988); shape of faecal pellets are species-specific and hence identification errors can be avoided. For each of these periods, six faecal samples per species for each habitat were collected in the south-eastern part of the Reserve – the area with the highest antelope density. The habitats were visited on foot and only fresh samples found were used. Maximally one sample per species was collected per site in order to avoid pseudoreplication. Sites were >3 km apart so that samples are assumed to represent different individuals of these territorial species (Lewis, 1994; de Jong *et al.*, 2004). Samples were collected on different sites within the Reserve in order to include regional variation, but sampling site was approximately consistent between seasons to be able to detect seasonal effects. The three main vegetation types cover approximately equal areas in the study area, and samples were only collected from the larger vegetation patches (>400 ha). Each sample was stored in a flask containing a mixture of formalin, acetic acid and alcohol.

Faeces were processed using standard laboratory techniques (Stewart & Stewart, 1970; Soane, 1980; Bhadresa, 1986). After processing, a subsample of each faecal sample was taken for a quantitative analysis of the epidermal fragments. The subsample was mounted on a counting chamber. Observations were made using a light microscope. The intersection points of counting chambers were used for quantification with the point-quadrat methodology. At each intersection point, overlying epidermal fragments were identified, comparing them with the reference collection. The percentage of monocots in the diet was calculated for Poaceae, Liliaceae and palms independently. Unidentified epidermis fragments were classified into two groups: dicots and monocots. A total of 100 epidermis fragments were identified per faecal sample, resulting in 600 identified fragments per antelope species per habitat per season.

Faecal density

In each of the three main vegetation communities, faecal densities were estimated on 20 linear transects, independent of the pellets collected for the faecal analysis. Transects were located at least 100 m from vegetation type boundaries, and followed for at least two hours; transect direction was set at each start to avoid crossing into other vegetation types, and bearing was maintained by compass. Transect length was measured with a pedometer and corrected for step length; total transect length varied from 4640 m in the sand forest to 9467 m in the savanna. All droppings encountered on both sides of the transects were identified to antelope species and perpendicular distance to the transect line was measured to the nearest centimetre.

Analysis

Cluster analysis is appropriate in detecting homogeneity between samples, such as to analyse similarity in diet composition between faeces from different antelopes collected in different vegetation types (Lepš & Šmilauer, 2003). An average linkage cluster analysis (computer program DENDRO, Schaffers, 1991) was used to analyse similarity in diet composition. Distance between samples was calculated using the quantitative Sorensen similarity index, calculating percentage similarity (PS) between samples:

$$\mathrm{PS} = 2 \times \frac{\sum_i (\min(p_{ia}, p_{ib}))}{\sum_i p_{iA} + \sum_i p_{iB}} \times 100\%,$$

where A and B are the two samples, and $\sum p_{iA}$ stands for the sum of the proportions of species i in sample A, and

$[\min(p_{ia}, p_{ib})]$ for the minimum proportion of species i that the two samples have in common.

A detrended correspondence analysis (DCA, DECORANA v2, ter Braak, 1986; Jongman *et al.*, 1995) was carried out to check for seasonal differences in diet.

As the three species occurred in the same habitats in the Maputo Elephant Reserve, we have taken dietary segregation as niche segregation. Diet breadth, representing diet diversity per faecal sample, was calculated following Nel (1978), based upon the niche breadth B of the Simpson's index of diversity, calculated from the proportion P in the diet of plant species i.

$$B = \frac{1}{\sum p_i^2}$$

Dietary overlap O_{ij} between antelope species i and j was calculated from the proportion of plant species k in the diet, following Pianka (1973):

$$O_{ij} = \frac{\sum (X_{ik} \cdot X_{jk})}{\sqrt{\sum X_{ik}^2 \cdot \sum X_{jk}^2}}$$

Diet exclusivity was measured as a proportion from the number of items only taken by one particular species relative to all dietary items taken by all three antelopes. An item was defined as a plant part of a specific species, i.e. taking leaf, root or fruit as separate diet items.

Differences in diet breadth in relation to species and season were tested using a two-factor ANOVA, as residuals followed a normal distribution, followed by a Tukey's multiple comparison test in SPSS (v12). Differences in the percentages of the diet comprising different species groups (monocots or exclusive species) over species and season were tested with a non-parametric two-factor tests (Zar, 1984), as data violated the assumption of normality.

Dropping density was computed by the computer program DISTANCE v 2.1 (Laake *et al.*, 1994; Buckland *et al.*, 2001), which corrects for differences in detection probability with increasing distance from the transect line. All distances of faecal pellets were included in the analysis, and no cut-off distance was applied. Faecal decay rates were assumed to be constant between the vegetation types. Distance is known to sometimes overestimate densities (Beavers & Ramsey, 1998; Cassey & McArdle, 1999), and it is therefore better to interpret results as relative density estimates. Non-parametric Spearman correlation tests were carried out to test for correlation between ranks of dietary items of different pairs of bovids.

Results

The cluster analysis showed that some individuals of the same bovid species had strikingly different diets in similar habitats, as revealed by faecal analysis (Fig. 1). Different linkage methods or ordination techniques (e.g. PRINCIPAL COMPONENT ANALYSIS, PCA, or DENTRENDED CORRESPONDENCE ANALYSIS, DCA) yielded a similar pattern (H.H.T. Prins, unpubl. data). A likely explanation is that individual animal movements took place on a shorter time scale than the passage rate of plant parts. Hence, we analysed only the average diet composition for each bovid species per season, by lumping the data from samples collected in different habitats in each season.

A wide range of dietary items was utilized by the three species. Over the whole year, this was 76 items for the common duiker, 80 items for the red duiker and 70 items for the suni, totalling 93 different items or 91 different plant species from a total of 109 different items available in the reference collection (Table 2). However, chi-squared tests found no significant difference between seasons (Table 1). For all three small bovids, the observed number of items in the diet was lowest during the dry season.

Diet breadth was lowest during the dry season (Table 1), and significant differences were reported for season ($F_{2,135} = 40.292$, $P < 0.001$), but not for species ($P > 0.05$). All three seasons were significantly different in diet breadth, with lowest values reported in the late dry season and highest values in the early wet season (Tukey's test, $P < 0.001$). Dietary specialization in the form of exclusive use by the different small bovids, was limited; on average only about 10% of the food items used by all three small bovids were specific to one species only (Table 1). The use of exclusive species was significantly larger in the dry season ($\chi^2 = 1306$, $P < 0.01$), and significantly larger for the red duiker, with lowest values recorded for the common duiker ($\chi^2 = 1537$, $P < 0.001$).

Major dietary shifts occurred for all antelopes over the year, as shown both by the cluster analyses (Fig. 1) and detrended correspondence analyses (Fig. 2). The proportion of Poaceae was unexpectedly high (>10%) for all three species (Table 1). This proportion declined significantly from the early wet season to the dry season ($\chi^2 = 1775$, $P < 0.001$), and was significantly smaller for red duiker ($\chi^2 = 1531$, $P < 0.001$).

Habitat overlap, as revealed by faecal sample density, appeared to be 100% for the two duiker species (Table 3). Faecal densities varied from 4153/ha for the red duiker in

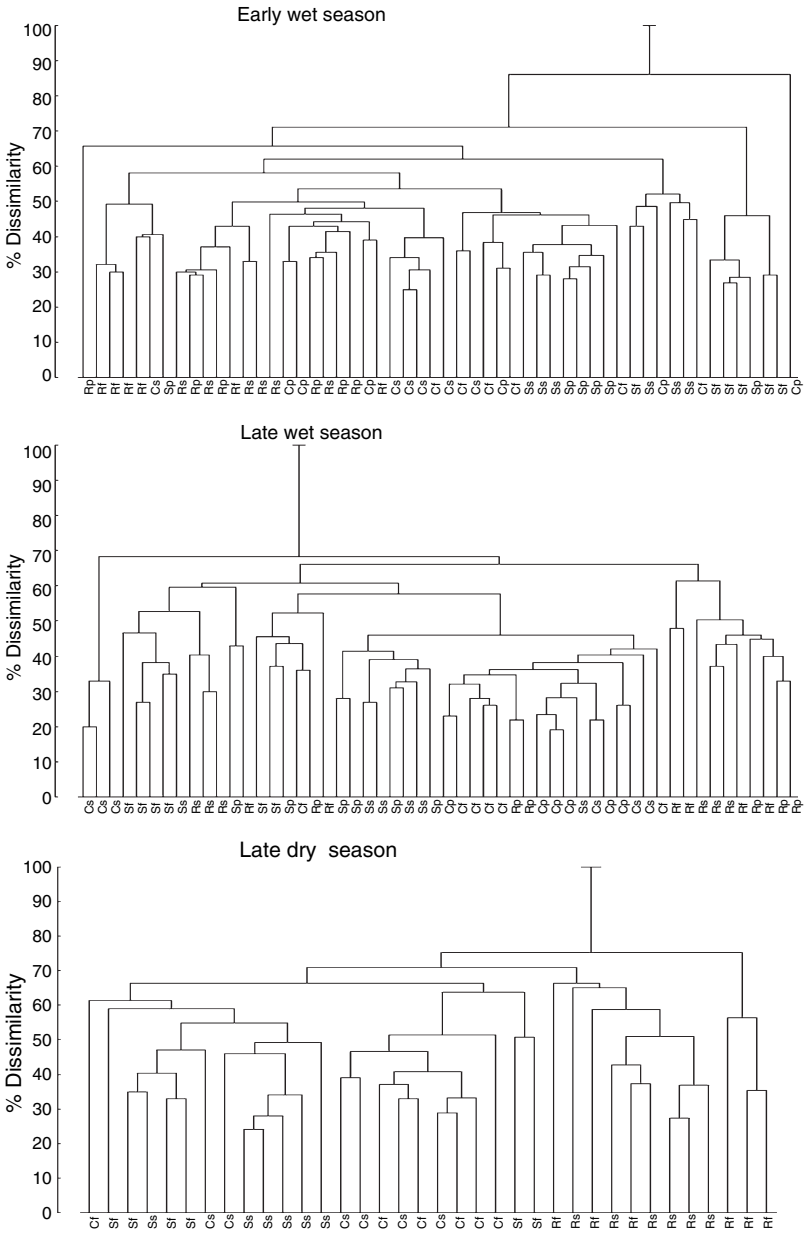

Fig 1 The results of average linkage cluster analysis illustrated by dendrograms highlighting the similarity between plant composition of faecal samples of antelope species collected in the different vegetation types. Sample codes refer to: C = common duiker; R = red duiker; S = suni; f = sand forest; s = savanna, p = grass plain.

the sand forests to 310/ha for the common duiker in the savanna. Confidence intervals were large, which is typical for the DISTANCE analysis. Suni apparently occurred infrequently in the savanna but commonly in the sand forest; on transect counts suni faecal pellets were not encountered on the savanna, although for the faecal analysis samples were also found for this species in the savanna and grass plains. On the basis of personal observations and discussions with the Park rangers, a fair estimate of the relative abundance of the three species is suni : red duiker : common duiker =1 : 2 : 4. Qualitative data (based on sightings and droppings) indicated that all three bovids occurred during the early and late wet season in all three habitats but were near to absent from the grass plain during the dry season.

Dietary overlap was relatively large during the early wet season, with 49% of the dietary items identical for all three species; during the late wet season, the overlap was approximately similar (53%), but it declined during the dry season to 25% (Table 1).

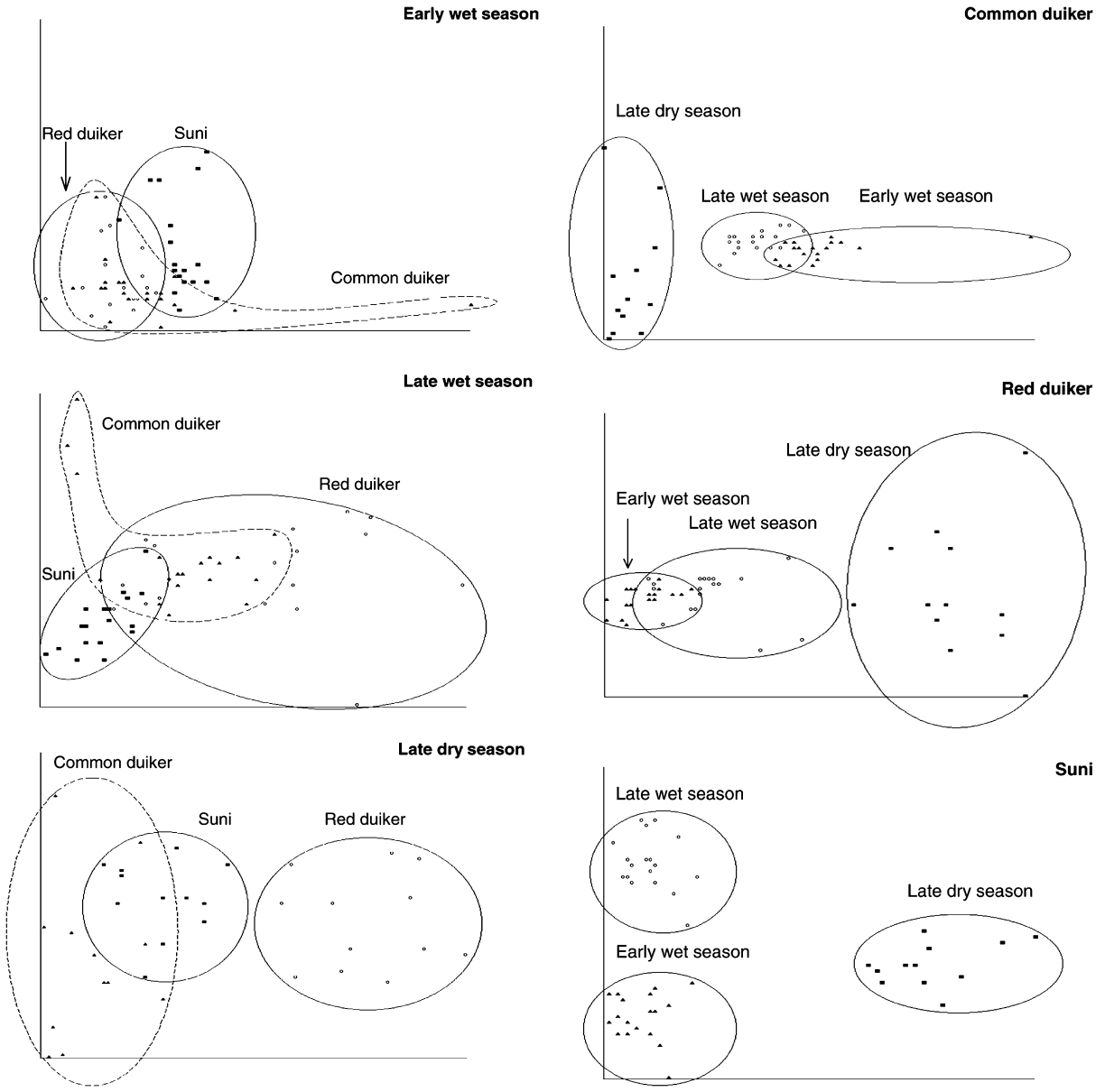

Fig 2 Biplots illustrating the results of detrended correspondence analysis. Dots represent faecal samples; ovals enclose samples collected in similar seasons or from similar antelope species. Results are both given per antelope species with rings around faecal samples collected in similar seasons, and per season with rings around faecal samples of each antelope species.

Dietary overlap, as measured by Pianka's formula, was relatively high between all species during both the early wet season and the late wet season with values ranging from 0.63 to 0.83. It declined during the dry season with values <0.38, showing that the diets became more segregated during periods of food scarcity (Table 1).

Discussion

Suni, red duiker and common duiker have all the same general feeding style – they are all concentrate selectors. Suni is slightly smaller than the duiker species, whereas the body weights of the duikers overlap. Ecological theory

predicts that if different species have the same feeding style and the same body mass, then these species should compete for food resources when they co-occur (Prins & Ol, 1998), or that competitive displacement should have taken place so that their diets show less overlap. For instance, Kingdon (1982) predicted habitat compression for the common duiker as the result of competition with other competing ungulates.

From our analyses, it is clear that all three antelope species had a wide diet selection, and did not concentrate their feeding efforts on one or a few species. Yet, some food items rank higher in the diet than others. How then are food items distributed between the three bovid species?

Kingdon (1997) suggested that the three species depend to a large extent on fallen leaves and fallen fruits. When there is no habitat segregation, as with the present three bovid species in the Maputo Elephant Reserve, and no interspecific exclusion through aggression (which has not been observed: Kingdon, 1982), one might expect scramble competition for these fallen items. Under scramble competition, food depletion takes place by the first individual, irrespective of species identity, that encounters a resource item (de Boer & Prins, 1990). If that were the case with the three small bovids concerned, then competition will not reveal itself with the type of data we have collected on dietary composition. Indeed, only differential population growth figures could then be taken as proof of competition. Our estimates of the relative abundance of the three species (suni : red duiker : common duiker = 1 : 2 : 4), would suggest common duiker to be superior in the competitive interaction. However, the question remains why suni and red duiker have not been outcompeted altogether? As the three species have been co-existing in the reserve for at least several decades (Tello, 1973), any competitive interactions between the three species may be weak. This argument is not changed by the

Table 1 Mean number of dietary items, diet breadth, exclusive use of food items (plant species or parts of specific plants), and percentage monocots (% Poaceae/Liliaceae/palms) in the diet of the three bovids based on faecal analysis (n = 18 faecal pellets or 1800 faecal fragments per species per season)

	Season			
	Early wet	Late wet	Dry	χ^2, *P*
Number of dietary items				
Common duiker	47	47	40	0.218, n.s.
Red duiker	49	62	45	0.794, n.s.
Suni	52	49	37	0.463, n.s.
Average	49	53	41	
Diet breadth, Simpson's *B*				
Common duiker	20	13	8	
Red duiker	17	19	15	
Suni	16	15	12	
Average	18	16	12	
Exclusive use of food items				
Common duiker	10%	6%	10%	
Red duiker	13%	14%	26%	
Suni	12%	8%	5%	
Average	12%	9%	14%	
Monocot occurrence (%)				
Common duiker	28/2/0	11/6/0	10/4/0	
Red duiker	16/4/0	8/5/2	16/4/0	
Suni	23/4/0	18/6/2	3/8/3	
Average	22/3/0	12/6/4	10/5/1	
Dietary overlap *O*				
Suni-Red duiker	0.63	0.66	0.37	
Suni- Common duiker	0.70	0.77	0.38	
Red duiker-Common duiker	0.83	0.70	0.21	

Dietary overlap *O* between pairs of small bovids in the Maputo Elephant Reserve over the three distinguished seasons. The chi-squared test tested for differences in diet composition among seasons per bovid species (df = 2). See Table 2 for a complete list.

Table 2 Diet composition of the three small bovid species per season, and sample sizes

	Early wet			Late wet			Dry		
Plant species	Red duiker	Common duiker	Suni	Red duiker	Common duiker	Suni	Red duiker	Common duiker	Suni
Acacia davyi	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.33	2.83
Acacia karroo	3.94	2.06	1.67	3.89	2.72	2.89	0.17	30.00	0.00
Acacia kraussiana	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00
Acacia sp.	1.94	2.33	2.06	3.89	4.33	1.61	2.92	0.17	0.58
Acacia xanthophloea	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	1.75
Afzelia quanzensis	6.72	2.67	3.00	9.89	5.28	2.56	0.08	1.67	6.33
Albizia adianthifolia	0.00	1.61	1.28	0.44	0.00	0.00	0.00	0.00	0.50
Albizia versicolor	0.00	0.00	0.00	1.28	0.06	0.00	0.00	0.00	0.00
Aloe bainesii	0.00	0.00	0.00	0.06	0.00	0.00	0.00	1.25	0.00
Aloe sp.	0.00	0.00	0.11	0.94	0.28	0.00	0.00	0.92	0.25
Andropogon eucomus	0.94	3.28	3.67	0.00	0.00	0.06	0.00	0.00	0.00
Andropogon gayanus	0.00	0.22	0.00	0.06	0.11	0.17	0.00	0.00	0.00
Androstachys johnsonii	0.00	0.00	0.06	0.39	0.17	0.00	1.08	0.33	0.75
Annona senegalensis	0.89	0.06	0.39	1.39	0.17	0.33	1.08	0.17	0.08
Apodytes dimidiata	2.39	2.67	3.50	3.39	2.94	0.83	0.00	5.08	0.25
Aristida canescens	0.00	0.28	0.33	0.00	0.00	0.28	0.00	0.00	0.00
Aristolochia sp.	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00
Artabotrys brachypetalus	0.39	1.83	0.06	0.28	0.33	0.00	1.83	1.08	1.67
Balanites manghamii	0.11	0.00	0.39	0.39	0.17	0.22	0.67	3.67	14.33
Boscia albitrunca	0.67	0.06	0.06	0.06	0.00	2.39	0.00	0.00	0.00
Brachylaena discolor	0.00	0.00	0.22	0.22	0.56	0.39	0.00	0.50	0.25
Bridelia micrantha	7.78	1.67	5.22	3.50	13.94	7.28	9.75	6.58	12.00
Canthium locuples	0.11	0.00	0.11	0.17	0.06	0.00	0.00	0.50	0.08
Capparis tomentosa	6.22	2.89	3.56	4.06	4.11	6.78	0.33	0.00	0.00
Clerodendrum glabrum	0.00	0.06	0.00	0.72	0.06	1.17	0.25	0.17	0.00
Combretum imberbe	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00
Combretum sp.	0.89	0.33	0.28	1.11	0.17	2.11	12.42	0.00	0.67
Commiphora neglecta	7.17	4.72	2.06	1.06	0.78	4.00	0.00	4.33	1.83
Crinum delagoense	0.00	0.00	0.00	0.00	0.00	0.00	1.50	0.00	1.67
Crotalaria monteiroi	0.00	0.00	0.00	0.06	0.00	0.06	1.58	0.08	0.00
Cymbopogon excavatus	1.17	1.94	0.17	1.00	2.50	6.61	2.33	0.00	0.00
Cynodon dactylon	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.42	0.00
Dialium schlechteri	0.06	0.50	0.56	0.89	0.39	0.11	0.75	0.00	0.00
Dialium sp. fruit	2.61	2.11	0.83	0.83	0.72	0.72	0.00	2.58	0.00
Un-id sp A.	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	1.00
Dichrostachys cinerea	1.06	2.17	0.28	6.61	1.11	0.78	3.83	6.33	3.83
Digitaria longiflora	0.83	5.72	3.78	0.17	0.00	0.17	0.00	0.00	0.00
Echinochloa pyramidalis	2.67	6.89	2.67	0.00	0.00	0.00	0.08	0.00	0.00
Euclea natalensis	0.00	0.00	0.33	2.06	0.56	0.33	0.08	1.08	1.67
Euclea sp.	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00
Eugenia capensis	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00
Euphorbia kunthii	0.17	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00
Euphorbia tirucalli	6.89	5.06	1.00	5.67	8.94	9.61	5.42	2.17	2.83
Festuca arundinacea	0.00	0.00	0.22	0.00	0.00	0.06	0.25	0.00	0.00
Ficus capensis	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00
Ficus sycomorus	0.33	0.11	14.00	0.22	0.33	0.83	3.25	1.17	7.25
Ficus spA.	0.28	0.33	2.39	0.44	0.56	0.00	0.00	0.00	0.83
Ficus spB.	0.00	0.00	0.00	0.00	0.06	0.00	1.83	0.00	0.00

Table 2 Continued

Garcinia livingstonei fruit	0.00	0.00	0.06	0.00	0.06	0.00	0.00	0.00	2.42
Grewia caffra	0.22	0.06	0.44	0.89	0.17	0.33	2.58	0.00	0.00
Hyparrhenia dissoluta	0.00	0.39	0.11	0.00	0.00	0.00	0.00	0.00	0.00
Hyparrhenia sp.	0.67	3.56	6.94	0.00	0.00	0.00	0.00	0.00	0.00
Hyphaene crinita	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25
Indigofera podophylla	0.00	0.00	0.00	0.06	0.00	0.00	5.75	0.00	0.00
Ischaemum arcuatum	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.83	0.00
Mangifera indica	0.22	0.00	0.00	0.22	0.11	0.00	0.00	0.00	0.00
Manihot esculenta	0.00	0.11	0.00	0.33	0.00	0.00	1.25	3.08	0.00
Mimusops caffra	0.28	0.00	0.00	0.39	0.00	0.06	2.00	1.17	0.17
Ozoroa obovata	0.00	0.00	0.00	0.00	0.00	0.06	0.92	0.00	1.25
Panicum maximum	0.89	0.67	0.39	0.00	0.00	0.00	0.00	0.00	0.00
Panicum sp.	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.00
Parinari capensis	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.67	0.00
Phoenix reclinata	0.00	0.00	0.00	0.06	0.00	0.11	0.00	0.00	0.00
Phragmites communis	0.00	0.44	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Phyllanthus reticulatus	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00
Rhus microcarpa	1.61	1.61	1.17	0.44	7.72	0.61	0.00	0.00	0.00
Rhus natalensis	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rhus sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00
Salacia kraussii	3.83	4.17	8.83	8.67	5.50	2.94	11.33	3.42	5.75
Sansevieria hyacinthoides	0.06	0.00	0.00	0.72	0.11	0.11	1.25	0.00	0.00
Sansevieria hyacinthoides rhizome	1.17	1.72	0.22	2.00	2.33	3.44	0.00	0.92	0.00
Sapium ellipticum	6.56	4.39	3.61	3.06	5.44	3.22	12.42	2.33	1.00
Scilla sp. root	0.00	0.00	0.00	0.00	0.00	0.28	0.00	1.33	0.83
Sclerocarya birrea	0.00	0.00	0.00	0.06	0.00	0.06	0.00	0.42	3.83
Sclerocarya birrea fruit	0.28	0.00	0.06	0.06	0.00	0.28	0.83	0.00	0.00
Scutia myrtina	1.06	1.00	0.11	0.11	0.00	0.17	0.08	0.83	2.83
Sesuvium portulacastrum	5.11	2.83	4.22	7.00	16.11	10.50	0.00	0.58	0.67
Setaria chevalieri	0.00	0.50	0.00	0.00	0.00	0.06	0.50	0.00	0.25
Setaria holstii	2.28	2.00	1.61	9.78	1.72	3.11	0.08	0.25	0.00
Sporobolus subtilis	0.00	0.22	0.06	0.00	0.00	0.00	0.00	0.00	0.00
Strychnos innocua	13.94	13.28	9.83	3.67	4.11	14.89	0.00	9.50	16.67
Strychos madagascariensis	0.33	0.00	0.00	0.17	0.94	0.06	0.00	0.00	0.00
Strychos spinosa	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Syzygium cordatum	0.00	0.00	0.00	0.28	0.17	0.00	1.00	0.75	0.58
Terminalia sericea	0.22	0.11	0.17	0.44	0.89	0.50	0.42	2.33	0.25
Themeda triandra	2.22	4.67	0.67	3.39	1.78	4.67	0.08	0.00	0.00
Triraphis schlechteri	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00
Vangueria infausta	0.50	0.00	0.61	0.11	0.50	0.11	0.00	0.00	0.00
Vangueria tomentosa	2.06	0.89	0.28	2.11	0.50	2.06	2.83	0.00	0.00
Vigna sinensis	0.00	0.00	0.00	0.06	0.00	0.00	0.50	0.67	0.00
Xylotheca kraussiana	0.06	0.00	0.00	0.06	0.00	0.00	2.67	0.00	0.00
Zea mays	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00
Ziziphus mucronata	0.06	5.33	6.22	0.33	0.17	0.06	1.00	0.00	0.00
Total	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00
Total number of identified fragments	600	600	600	600	600	600	600	600	600

The percentage of each diet item is given in relation to the all diet items encountered for that particular antelope species and that particular season.

Table 3 Mean faecal density in samples/ha (and 95% confidence interval) of the three small bovids in the Maputo Elephant Reserve, together with mean transect length

	Sand forest	Savanna	Grass plains
Common duiker	1415 (350–5723)	310 (27–3507)	0
Red duiker	4153 (3451–4995)	1224 (340–4408)	0
Suni	1454 (225–9379)	0	0
Transect length (m) mean	4640	9467	7808

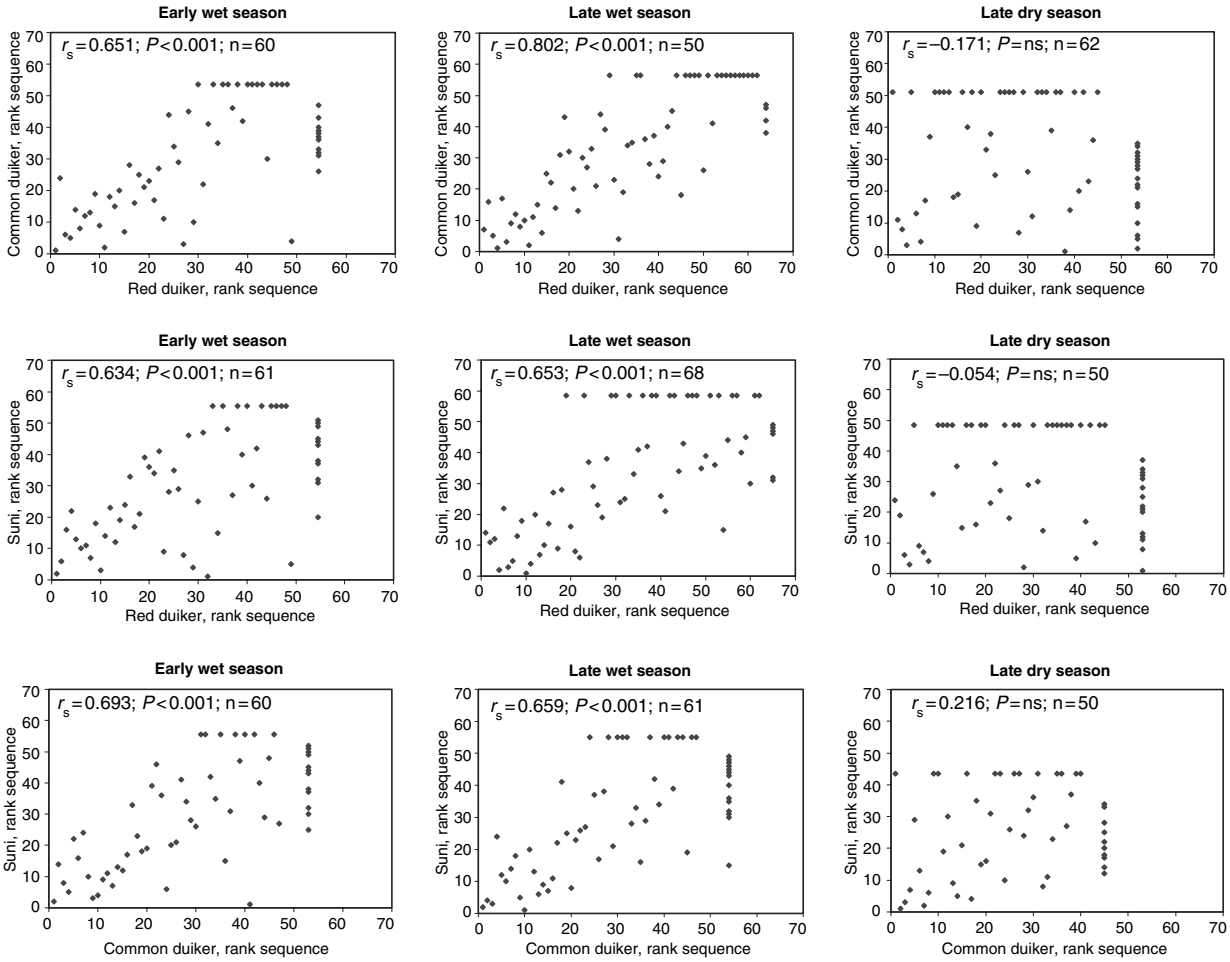

Fig 3 Correlation between the ranks of dietary items of different pairs of small bovids species per season. Non-parametric Spearman's correlation test results are illustrated in each graph, with correlation coefficient, r_s, significance level P, and sample size 'n'

observation that the three small bovids not only included fallen leaves and fruits in their diet but also foraged to a considerable extent on monocots (Table 1). Gagnon & Chew (2000) reported percentage of monocots in the diet of red duiker, common duiker, and suni of 1%, 12%, and 6%, respectively, whereas we found between 15% and 20% for the red duiker (Table 1), 14% and 30% for the common duiker, and 14% and 27% for the suni.

The results also do not point in the direction of competitive displacement so that the three species utilize a different food spectrum. Indeed, the degree of dietary specialization is very low (Table 1), only some 10% of the food items were exclusively used by each species during the different seasons. This might be enough to allow co-existence, if the food items that are used exclusively are abundant in the environment. However, dietary segregation was significantly

highest during the dry season (Table 1), and the highest proportion of exclusive use was also reported in the dry season (i.e. 26% for the red duiker). This implies that some niche segregation occurred during the dry season. Hence, the dry season data showed evidence for a potential competition bottleneck. Niche segregation, however, is mainly on quantitative use of the vegetation and not based on absolute exclusion (Tables 1 and 2). Generally, the dry season is the period of scarcity for savanna-adapted herbivores (Beekman & Prins, 1989; Prins, 1996; Traill, 2004). Thus, if resource competition occurs, it is likely to be limited to the dry season. Hence, the problem of co-existence of the three near-identical concentrate selectors may be explained by niche segregation in the dry season only.

However, before it can be concluded that the observed niche segregation during the dry season reduces resource competition, it should be proven that there is resource limitation during that time of the year. If there is no resource limitation, niche segregation can be the result of adaptation as the ghost of competition past. The species might be resource-limited because they are not limited by predation (see Krebs *et al.*, 1998). Indeed, large predators and birds of prey are near to absent from the Reserve, and poaching of these small bovids is probably not a major problem inside the Reserve (W. F. de Boer, pers. obs.).

There are, however, several arguments against resource competition. First, resource segregation was mainly quantitative but not absolute (Table 1). Secondly, the detrended correspondence analysis (Fig. 2) showed a large overlap in diet composition, even in the dry season. Thirdly, the Reserve experienced severe depletion of its large herbivores. It is known elsewhere, that extermination of large herbivores has led to an increase of duikers in African savannas (C. Child, pers. comm.). This has been ascribed to a release from resource competition from other herbivores (Kingdon, 1982). This has been observed in other African herbivores too, and ungulates appear to compensate for fluctuations of other species within their assemblage (Prins & Douglas-Hamilton, 1990). It appears that these duikers also experienced this decrease of competition from other herbivores, although the impact of competition with hippos *Hippopotamus amphibius* L., or smaller herbivores (chacma baboon *Papio ursinus* Kerr, cane rats *Thryonomys swinderianus* Temminck) remains to be quantified.

If it is then concluded that there is little evidence for pronounced competition between suni, red duiker and common duiker in the Reserve since these species were released from competition with other herbivores, we ask what model would best describe niche segregation (Tokeshi, 1997) between the three species. If the rank sequence of dietary items reflects preference, or dietary need, we can assume that because the three small bovids are so similar, they would have identical rank-frequency distributions if there is no competition. If the three species distributed the available niche equally among them, we would expect that the rank of importance in the diet to show a positive correlation. Indeed, during the wet season, the rank sequence of items in the diets of the three bovids shows a high correlation (Fig. 3). However, during the dry season at the time of the inferred scarcity, when the three species show niche segregation (Table 1), it appears that they have a random apportionment of dietary items, and it can therefore not be interpreted as the result of competitive displacement. Niche segregation at this time of the year is not the result of competition.

Acknowledgements

We are grateful to the Direcção Nacional de Florestas e Fauna Bravia, and the staff of the Maputo Elephant Reserve, who granted us permission to work in the Maputo Elephant Reserve. We are also grateful to Carlos Boane, Júlio Dungo and João Cuna who helped with the identication of the plant material, to John Hatton and Manuel Vidal who offered additional guidance, and to two unknown reviewers for there comments. The research was carried out within the framework of the Deibi Project.

References

Beavers, S.C. & Ramsey, F.L. (1998) Detectability analysis in transect surveys. *J. Wildl. Manag.* **62,** 948–957.

Beekman, J.H. & Prins, H.H.T. (1989) Feeding strategies of sedentary large herbivores in East Africa, with emphasis on the African buffalo. *J. Afr. Ecol.* **27,** 129–147.

Belovsky, G.E. (1986) Generalist herbivore foraging and its role in competitive interactions. *Am. Zool.* **26,** 51–69.

Bhadresa, R. (1986) Faecal analysis and exclosure studies methods. In: *Plant Ecology* (Eds P. D. Moore and S. D. Chapman). Blackwell Scientific Publications, Oxford.

de Boer, W.F. & Prins, H.H.T. (1990) Large herbivores that strive mightily but eat and drink as friends. *Oecologia* **82,** 264–274.

de Boer, W.F., Ntumi, C., Correia, A. & Mafuca, J. (2000) Diet and distribution of elephants in the Maputo Elephant Reserve. *Afr. J. Ecol.* **38,** 188–201.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L. (2001) *Introduction to Distance Sampling:*

Estimating Abundance of Biological Populations. Oxford University Press, Oxford.

CASSEY, P. & MCARDLE, B.H. (1999) An assessment of distance sampling techniques for estimating animal abundance. *Environmetrics* **10**, 261–278.

CONNELL, J.H. (1980) Diversity and the coevolution of competitors, or the ghost of the past. *Oikos* **35**, 131–138.

DNFFB (1997) *Plano de Maneio, Reserva Especial de Maputo, 1997–2001; Volume 2: Informação de Base*. Direcção Nacional de Florestas e Fauna Bravia, Maputo.

ESTES, R.D. (1991) *The Behavior Guide to African mammals, Including Hoofed Mammals, Carnivores, Primates*. University of California Press, Berkeley, CA.

FIELD, C.R. (1972) The food habits of wild ungulates in Uganda by the analysis of stomach contents. *East. Afr. Wildl. J.* **10**, 17–42.

GAGNON, M. & CHEW, A.E. (2000) Dietary preferences in extant African Bovidae. *J. Mammal.* **81**, 490–511.

HOFMANN, R.R. (1973) *The Ruminant Stomach: Stomach Structure and Feeding Habits of East African Game Ruminants*. East African Literature Bureau, Nairobi.

JARMAN, P.J. (1974) The social organization of antelope in relation to their ecology. *Behaviour* **48**, 215–267.

JARMAN, P.J. & SINCLAIR, A.R.E. (1979) Feeding strategy and the pattern of resource partitioning in ungulates. In: *Serengeti: Dynamics of an Ecosystem* (Eds A. R. E. SINCLAIR and M. NORTON-GRIFFITHS). University of Chicago Press, Chicago, pp. 130–163.

JENKINS, K.J. & WRIGHT, R.G. (1988) Resource partitioning and competition among cervids in the northern Rocky Mountains. *J. Appl. Ecol.* **25**, 11–24.

DE JONG, C.B., VAN WIEREN S.E., GILL, R.M.A. & MUNRO, R. (2004) Relationship between diet and liver carcinomas in roe deer in Kielder Forest and Galloway Forest. *Vet. Rec.* **155**, 197–200.

JONGMAN, R.H.G., TER BRAAK, C.J.F. & VAN TONGEREN, O.F.R. (1995) *Data Analysis in Community and Landscape Ecology*. Cambridge University Press, Cambridge.

KEIPER, R.R. (1985) Are sika deer responsible for the decline of white-tailed deer on Assateague Island, Maryland. *Wildl. Soc. Bull.* **13**, 144–146.

KINGDON, J. (1982) *East African Mammals: An Atlas of Evolution in Africa, Vol III Part C (Bovids)*. Academic Press, London.

KINGDON, J. (1997) *The Kingdon Field Guide to African Mammals*. Academic Press, San Diego, CA.

KREBS, C.J., SINCLAIR, A.R.E., BOONSTRA, R., BOUTIN, S., MARTIN K. & SMITH, J.N.M. (1998) Community dynamics of vertebrate herbivores – how can we untangle the web. In: *Herbivores, between Plants and Predators; Symposia of the British Ecological Society 38* (Eds H. OLFF, V. K. BROWN and R. H. DRENT). Blackwell Science, Oxford.

LAAKE, J.L., BUCKLAND, S.T., ANDERSON, D.R. & BURNHAM, K.P. (1994) *Distance Sampling; Abundance Estimation of Biological Populations, DISTANCE User's Guide, Version 2.1*. Colorado Cooperative Fish and Wildlife Research Unit, Fort Collins, CO.

LAWSON, D. (1989) The food habits of suni antelopes (*Neotragus moschatus*) (Mammalia: Artiodactyla). *J. Zool.* **217**, 441–448.

LEPŠ, J. & ŠMILAUER, P. (2003) *Multivariate Analysis of Ecological Data using Canoco*. Cambridge University Press, Cambridge.

LEWIS, S.W. (1994) Fecal and rumen analyses in relation to temporal variation in black-tailed deer diets. *J. Wildl. Manag.* **58**, 53–58.

LOFT, E.R., MENKE, J.W., KIE, J.G. & BERTRAM, R.C. (1987) Influence of cattle stocking rate on the structural profile of deer hiding cover. *J. Wildl. Manag.* **51**, 655–664.

LOFT, E.R., MENKE, J.W. & KIE, J.G. (1991) Habitat shifts by mule deer: the influence of cattle grazing. *J. Wildl. Manag.* **55**, 16–26.

MATHUR, V.B. (1991) Ecological Interaction between Habitat Composition, Habitat Quality and Abundance of some Wild Ungulates in India. DPhil. thesis. Oxford University, Oxford.

MATTHEWS, W.S, VAN WYK, A.E, VAN ROOYEN, N, BOTHA, G.A (2001) Vegetation of the Tembe Elephant Park, Maputaland, South Africa. *S. Afr. J. Bot.* **67**, 573–594.

MISHRA, C., VAN WIEREN, S.E., KETNER, P., HEITKONIG, I.M.A. & PRINS, H.H.T. (2004) Competition between domestic livestock and wild bharal *Pseudois nayaur* in the Indian Trans-Himalaya. *J. App. Ecol.* **41**, 344–354.

NEL, J.A.J. (1978) Habitat heterogeneity and changes in small mammal community structure and resource utilization in the southern Kalahari Ecology and Taxonomy of African Small Mammals. In: *Bulletin of Carnegie Museum of Natural History 6* (Ed. D.A. SCHLITTER). Carnegie Museum of Natural History, Pittsburgh, PA.

PIANKA, E.R. (1973) The structure of lizard communities. *Annu. Rev. Ecol. Syst.* **4**, 53–74.

PRINS, H.H.T. (1996) *Behaviour and Ecology of the African Buffalo: Social Inequality and Decision Making*. Chapman and Hall, London.

PRINS, H.H.T. (2000) Competition between wildlife and livestock. In: *Wildlife Conservation by Sustainable Use* (Eds H. H. T. PRINS, J. G. GROOTENHUIS and T. T. DOLAN). Chapman and Hall, London.

PRINS, H.H.T. & DOUGLAS-HAMILTON, I. (1990) Stability in a multi-species assemblage of large herbivores in East Africa. *Oecologia* **83**, 392–400.

PRINS, H.H.T. & OLFF, H. (1998) Species richness of African grazer assemblages: towards a functional explanation. In: *Dynamics of Tropical Communities; Symposia of the British Ecological Society 37* (Eds D. M. NEWBERY, H. H. T. PRINS and N. D. BROWN). Blackwell Science, Oxford.

PUTMAN, R.J. (1996) *Competition and Resource Partitioning in Temperate Ungulate Assemblies*. Chapman and Hall, London.

RAGOTZKIE, K.E. & BAILEY, J.A. (1991) Desert mule deer use of grazed and ungrazed habitats. *J. Range Manag.* **44**, 487–490.

RITCHIE, M.E. & OLFF, H. (1999) Spatial scaling laws yield a synthetic theory of biodiversity. *Nature* **400**, 557–560.

SCHAFFERS, A. (1991) *DENDRO; a Computer Program Generating Dendrograms, using Various Indices of Similarity and Methods of Clustering*. Wageningen University, Wageningen.

SOANE, G.A. (1980) Food Selection by the Rabbit. PhD thesis, University College of North Wales, Bangor.

SOMERS, M., RASA, O.A.E. & APPS, P.J. (1990) Marking behavior and dominance in suni antelope (*Neotragus moschatus*). *Z. Saeugtierk.* **55,** 340–352.

STACE, C.A. (1965) Cuticular studies as an aid to plant taxonomy. *Bull. Br. Mus. (Nat. Hist.) Bot* **4,** 1–78.

STEWART, D.R.M. & STEWART, J. (1970) Food preference data by faecal analysis for African plains ungulates. *Zool. Afr.* **15,** 115–129.

TELLO, J.L.P.L. (1973) Reconhecimento ecológico da Reserva dos Elefantes do Maputo. *Rev. Vet. Moç.* **5/6,** 1–186.

TER BRAAK, C.J.F. (1986) Canonical correspondence analysis: a new eigenvector method for multivariate direct gradient analysis. *Ecology* **67,** 1167–1179.

TOKESHI, M. (1997) Species coexistence and abundance: patterns and processes. In: *Biodiversity, an Ecological Perspective* (Eds T. ABE, S. A. LEVIN and M. HIGASHI). Springer, New York.

TRAILL, L.W. (2004) Seasonal utilization of habitat by large grazing herbivores in semi-arid Zimbabwe. *S. Afr. J. Wildl. Res.* **34,** 13–24.

VOETEN, M.M. & PRINS, H.H.T (1999) Resource partitioning between sympatric domestic herbivores in the Tarangire region of Tanzania. *Oecologia* **120,** 287–294.

WALKER, C. (1988) *Signs of the Wild,* 4th edn. National Book Printers, Cape Town.

ZAR, J.H. (1984) *Biostatistical Analysis,* 2nd edn. Prentice Hall, Englewood Cliffs, NJ.

(Manuscript accepted 16 November 2005)

